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NEWLY ESTABLISHED FAMILIES OF THE ORDER BRANCHIOBDELLIDA (ANNELIDA: CLITELLATA) WITH A SYNOPSIS OF THE GENERA

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Abstract.—General remarks and a brief survey of the branchiobdellid literature are followed by a review of the group's taxonomic characters, methods of study and speculations as to its origins. A key to newly recognized families and eighteen genera is given. The order is divided into five families: Branchiobdellidae, Bdellodrilidae, Xironodrilidae, Caridinophilidae, Cambarincolidae. A synopsis of the genera is included with the familial diagnoses.

The annelid worms of the order Branchiobdellida are currently attracting a modest degree of attention. Since 1950, nine of the eighteen genera and more than eighty of their 132 included species have been diagnosed. The opinion once held that the branchiobdellidans are a homogeneous group (Stephenson 1930:796) has long since been abandoned; their former association with either the Hirudinea or Oligochaeta has been dissolved (Holt 1965b).

This proliferation of taxa and the recognition of the structural diversity expressed thereby now make it appropriate to segregate the genera of this previously monotypic order into families and to present a synopsis of the included genera. A brief summary of branchiobdellidan natural history will be followed by a review of selected literature devoted to them, a consideration of the methods and anatomical characters that have been used in taxonomic studies of them and a discussion of the group's origin and distribution. This introduction is followed by keys to the families and genera and diagnoses of these taxa with illustrations, literature citations, number of included species and geographical range. It is to be emphasized that these efforts should be considered as provisional and transitional in nature: probably much less than half of the world fauna of the worms is known.

The branchiobdellidans are obligate symbionts of Holarctic (with limited excursions into the borders of the Neotropical and Oriental regions in Central America and China) freshwater crustaceans (crayfish, crabs, shrimps and isopods) that move in a leech-like fashion over the bodies of their hosts and feed on a variety of substances: the host's blood, eggs and (?) young, other external symbionts and, most often, the bacterial and algal gloea that often covers the host's body. Among those found on astacoidean crayfishes, different species tend to occur on different regions of the host animal and their feeding habits may reflect their occupancy of these microhabitats.

Nearly all astacoideans carry these symbionts. Although there is no known species-to-species host specificity, some branchiobdellidans, e.g., the isopod egg-eating *Cambarincola aliena* Holt, 1963, may be restricted to a single species of host because of such feeding adaptations. Branchiobdellidans have been rather diffidently reported as living away from any host (Holt 1973a: 152–159), but there is no record of them depositing cocoons except on the host's body. The first report of branchiobdellidans from other than astacoidean hosts (Hobbs and Villalobos 1958) was followed by the additions of several such instances: freshwater crabs in Central America, Mexico and

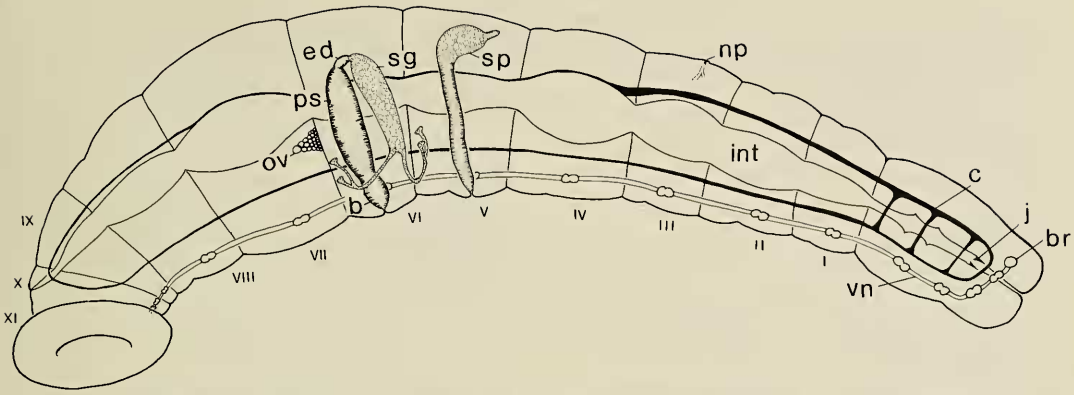

Fig. 1. Generalized branchiobdellid. Abbreviations: I–XI, trunk segments; b, bursa; br, brain; c, circulatory system; ed, ejaculatory duct; int, intestine; j, jaws; np, nephridiopore; ov, ovary; ps, penial sheath; sg, spermiducal gland; sp, spermatheca; vn, ventral nerve cord (from Holt 1969).

Louisiana; troglobitic isopods from Tennessee and Mexico; pseudothelphusid crabs from Central America and Mexico; freshwater shrimps from China. These instances seem to be from unusual habitats (caves) or from regions at the periphery, or beyond (Nicaragua and Costa Rica), of the range of the usual hosts. Little is known of other aspects of the life history, ecology, and physiology of these worms. Some studies of their natural history are marred by improper or inadequate taxonomic determinations.

The taxonomy of the group is incomplete and in some ways unsatisfactory simply because a large proportion of the branchiobdellidan fauna is undescribed: many new forms are known to await diagnosis in the collections of the National Museum of Natural History of the Smithsonian Institution.

A brief history of studies of the branchiobdellidans. —Only the major taxonomic works are considered herein; other references may be found in them.

In Europe, the number of nominal species of the genus *Branchiobdella* Odier, 1823, had reached forty-three when Pop (1965) reduced it to four species, one with three subspecies. This is almost surely an extreme example of "lumping," but there are probably only a few species of branchiobdellidans in Europe.

The Japanese and Korean branchiobdellidan fauna was studied by Yamaguchi (1934). A few species have been recognized by Chinese workers (Liang 1963; Liu 1964, 1984; Liu and Chang 1964; Liu and Zhang 1983). The Asiatic fauna, as now known, consists of 32 species assigned to six genera (two of these genera are new ones to be proposed by Gelder and Liu (pers. comm.) and one is the North American genus *Cambarincola* represented by the introduced *C. okadai* Yamaguchi, 1933).

The principal homeland of the branchiobdellidans is North America. Important early contributions to a knowledge of these worms were made by Moore (1895b) in his anatomical study of *Bdellodrilus illuminatus,* which has served as a model for all subsequent such studies, and the recognition of new forms (Moore 1894, 1895a). Ellis (1912, 1918, 1919) diagnosed the genera *Cambarincola* (1912), *Xironodrilus* (1918), and *Xironogiton* (1919) and recognized a total of seven new species in these and other genera. Hall (1914) raised the family Branchiobdellidae to the status of a superfamily and erected the genus *Ceratodrilus.* Goodnight (1940) assembled these works and others, divided the Branchiobdellidae into two subfamilies and added some generic diagnoses and species descrip-

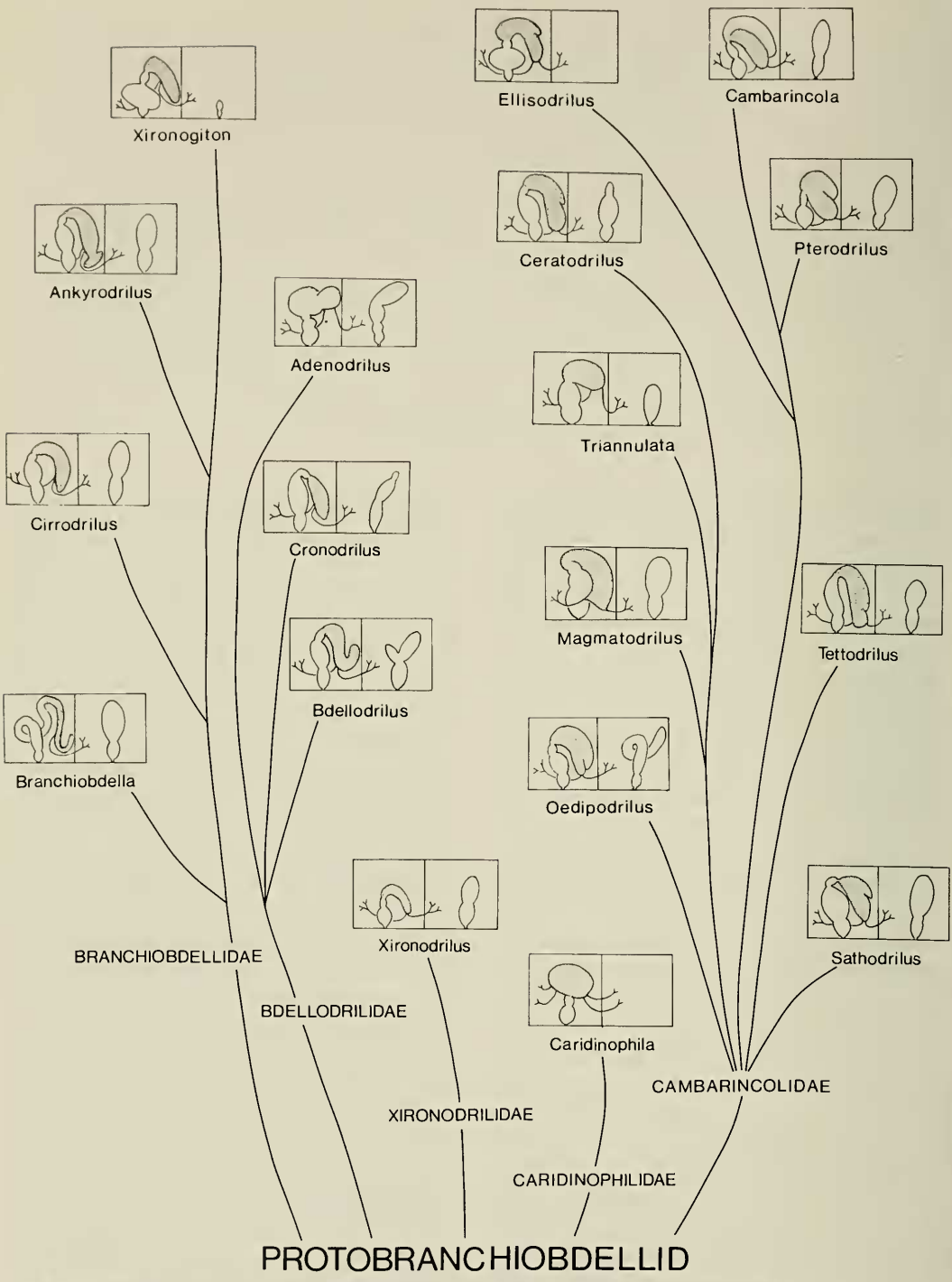

Fig. 2. Suggested relationships of the genera and families of the order Branchiobdellida.

tions. Hoffman (1963) treated 21 species, 12 of them new, in his monograph of the genus *Cambarincola* which also contains important reflections on taxonomic characters. Holt (1949) demonstrated the importance of the reproductive systems as a source of taxonomically important characters. Since then, he has described 55 new species and erected eight new genera (Holt 1960b, 1965a, 1967a, b, 1968b, 1977b) and published monographs of the genera *Pterodrilus* (Holt 1968c) and *Xironogiton* (Holt 1974b). The argument for raising the family Branchiobdellidae to ordinal rank (Holt 1965b) was followed by a review that is semipopular in style (1968a) and zoogeographic treatments (Hobbs et al. 1967, Holt 1969), among other studies.

Methods of collection, preservation and preparation for study.—An inhibiting factor in the study of the branchiobdellidans is the difficulty of doing anatomical studies of them. The worms range from about one to six millimeters in length (when contracted) and are opaque unless special methods are used. The preparation of serial sections is often hampered by the presence of diatoms in the gut, but it is essential that beginning students familiarize themselves with the basic anatomy of the animals by studies of such sections and of dissections. The preparation of stained whole mounts of the animals requires live specimens to be relaxed (? with 1–5% magnesium chloride), fixed and stained. The more usual method is to dehydrate specimens in ethanol, clear in clove oil and mount unstained in Canada balsam. Microscopic study of specimens so treated requires the use of an objective for the microscope that is adjusted to an unusually long working distance (approximately 1.5 mm) that enables the student to see through the total thickness of the worm or to turn over the slide on which it is mounted in order to view it from both sides.

Another nuisance occurs because much of the material presented to the student has been taken from the sediment at the bottom of jars in which crayfish have been collected. The students of crayfish usually preserve their animals in 70% ethanol and jam all the crayfish they can find into a collecting jar. The result is rotten worms often totally useless for serious study. For the best results, using the method described above, the branchiobdellidans should be preserved in 5% formalin in 70% ethanol and the collecting jars should not be overcrowded.

Taxonomic characters.—The students of the branchiobdellidans have used a number of features as taxonomic characters. To evaluate these usages a brief description of a generalized branchiobdellidan (Fig. 1) is required. The body consists of 15 segments of which four constitute a head and the remainder a trunk with a terminal sucker. Only the post-cephalic body segments have traditionally been numbered.

The prostomium is absent and the first cephalic segment, the peristomium, is usually divided into upper and lower lips which may be further subdivided into lobes; occasionally lateral lobes are present. The upper lip in some forms may be furnished with digitate projections or tentacles. The body segments are indicated externally by intersegmental furrows and are usually subdivided by a circular groove which produces a secondary annulus. The anterior annulus of some segments in some species is greater in diameter than the secondary annulus: there are "dorsal ridges." The dorsal ridges may carry fan-like or finger-like projections. The greater diameter of the anterior annuli in these cases is produced by the insertion of slips of the longitudinal segmental muscles into the outer body wall posterior to the intersegmental furrows and into the secondary furrow that delimits the posterior, secondary annulus, or sometimes in front of this furrow (Holt 1960b:fig. 7). The body outline is said to be smooth if the dorsal ridges are absent. The anterior nephridia open on segment III through two dorsolat-

eral pores or by a median dorsal pore. The anus opens dorsally on what apparently is always segment X. The posterior sucker (the peristomium forms an anterior one) is formed from the eleventh segment with, apparently, in some cases portions of segment X included. Both suckers are aided in their function by glandular secretions (Weigl 1980). Three otherwise dissimilar genera are characterized by a dorsoventral flattening of some of the mid-body segments.

The nervous and circulatory systems are annelidan, apparently invariant, and rarely mentioned in taxonomic works. The digestive system likewise presents few features of taxonomic interest: the gut is expanded much more noticeably in some segments of dorsoventrally flattened forms, the pharynx has one or more expansions (pharyngeal sulci); and all branchiobdellidans possess, dorsally and ventrally, pharyngeal placoids (jaws) that normally bear teeth and that vary in shape, size and number of teeth. Oral papillae, thought to be sensory in function, surround the mouth opening in several forms. However, it is possible that these small structures are present in most branchiobdellidans and because of their size have been simply overlooked in the descriptions of many species.

There are two pairs of nephridia. An anterior pair lies asymmetrically alongside the gut in segments I–IV, and discharges to the exterior on segment III. Variation in the position of anterior nephridia may exist among members of a species or between species (Moore 1897:329–330), but this possibility has not been further investigated. The posterior pair lie, one on each side, in segment VIII (Moore 1897:332) and open on the anterior lateral surface of segment IX (Freeman 1963).

The female reproductive system consists of paired ovaries, placed laterally on the posterior face of septum 6/7 and a spermatheca in segment V. There are no oviducts; eggs are expelled through a pair of ventrolateral pores in the body wall of segment VII. The spermatheca opens by a median pore on the venter of segment V and is a blindly ending sac that may be variously modified along its length. The epidermis of segments VI and VII is provided with glands forming a mucus-secreting clitellum.

The male system is more complex. Two pairs of testes located on the posterior faces of septa 4/5 and 5/6 break up at maturity into morulae that release spermatozoa into the body cavity. Paired male funnels in the posteroventral quadrats of the testicular segments open into thin ducts, the vasa efferentia, that unite to form vasa deferentia. The latter fuse to form a glandular organ, the spermiducal gland, which may have a diverticulum of greater or lesser distinctiveness, the prostate. In most forms a muscular tube joins the spermiducal gland to the penial sheath, the ental part of the bursa, which encloses the penis. The latter projects into a cavity, the bursal atrium, which opens mid-ventrally on segment VI. The penis takes several forms: in some genera it is eversible, consisting of a cuticular tube with or without hooks and with or without strands (presumably muscular) that attach it to the inner wall of the penial sheath. In other forms it is clearly muscular and is protruded by the eversion of the wall of the atrium as a cone-shaped mass. In some species this mass is narrowed and similar in composition and apparent eversibility to those of species in which a clearly eversible penis has strands connecting it to the inner wall of the penial sheath (Holt 1982:254–255).

There are numerous permutations of the elements of the reproductive systems, of the variations of the jaws and their teeth and of the features of the body surface. Most of the variations in structure shown by the branchiobdellidans are stable and discontinuous and no instance is now known with certainty of North American species that gradually vary in space. Consequently no subspecies of these have been recognized (but cf. *Cambarincola osceolai* Hoffman, 1963:331).

Some variations in body form are obvious adaptations to a particular way of life, but nothing can be said about the significance of most of the differences in structures that are used in the taxonomy of the group.

Members of a genus usually present a common facies, although interspecies differences are common in some external features (for example, the presence or absence of peristomial tentacles or dorsal ridges which occur within the confines of a single genus). Two of the three dorsoventrally flattened genera and several terete ones cannot be separated on the basis of external appearance and recourse must be had to features of the male reproductive system to do so. The same is true of the jaws: although members of a genus share a basic plan of jaw structure, one type of jaw may be shared by several genera. The number of anterior nephridiopores (one or two) are of necessity shared by several genera. Supraspecific taxa must, perforce, be based on modifications of the male reproductive system.

There have been other discussions of taxonomic characters used in studies of the branchiobdellidans (Hoffman 1963; Holt 1953, 1960a, 1965a, 1968a, b, 1973c; Holt and Hoffman 1959, inter alia) and suppositions expressed as to "primitive" as opposed to "advanced" characters (cf. Holt 1973c:3). These efforts, however, have been directed to features diagnostic of both genera and species. Herein attention will be directed to features that characterize genera and suprageneric taxa and many features used in the diagnosis of species ignored. Their usage may be derived from the taxonomic works cited above.

Of the somatic (non-genitalic) characters, only one is important in the present context. (The shape of the jaws has not been carefully considered, though Ellis (1919:241–243) laid the basis for a system utilizing the jaws). The ancestral branchiobdellidans probably were provided with separate openings of the anterior nephridia: five genera are so characterized; the remaining genera have a common opening (one anterior nephridiopore). In all cases, these openings, whether one or two, are obscure pores on the dorsum, or latero-dorsum, of segment III. In two of these five genera the middle segments are dorsoventrally depressed, but there is no reason to believe that there is any phylogenetic relationship between the presence of two anterior nephridiopores and a depressed body form (segment III of all branchiobdellidans is terete).

There is no way of knowing, except by uncertain inferences, the anatomical shapes and relationships of the components of the reproductive systems of the ancestors of the branchiobdellidans. Among living forms, the female system is relatively invariant. The spermatheca may be absent, reduced to vestigialness or "bifid" (having a lateral branch). Otherwise the variations in the presence or absence of an ental bulb, the shape of the spermathecal bulb (the sperm-storing part of the organ) and of the ectal spermathecal duct and bursa are only uncertainly, and in not all cases, associated with groups of species forming genera.

This is not true of the male system. The testes may consist of one or two pairs. The vasa deferentia may enter the spermiducal gland ectad to its inner end or entally and there may or may not be a prostate or rudiment thereof associated with it. The penis is variable in its structure. The composition of its wall ranges from a cuticular tube, with or without hooks, to a dense cone-shaped mass of muscle: the former type is eversible; the latter protrusible.

There are left, then, relatively few features whose states may serve to characterize suprageneric groupings and presumptively "primitive" characters (Holt 1968a:83–84) are found in more than one of any possible groupings of genera. Whether there are one or two nephridiopores; the number of pairs of testes and their location; the nature of the junction of the vasa deferentia with the spermiducal gland; the presence or absence of a prostate associated with the spermi-

Table 1.—Data matrix for some major characters.

	Caridinophilidae	Cambarincolidae	Xironodrilidae	Bdellodrilidae	Branchiobdellidae
Spermiducal gland: globose → elongate	globose	elongate	elongate	elongate	elongate
Vasa deferentia enter spermiducal gland: terminally → subterminally	—	terminally	terminally	subterminally	subterminally
Spermatheca: present → absent	absent	absent-present	present	present	present
Mid-body depression: present → absent	absent	absent	present	absent	absent-present
Anterior nephridiopores: 2 → 1	1	1	2	1	2
Prostate: absent → present	absent	absent-present	absent	absent	absent
Testes 2 pairs → 1 pair	2	2	2	2	1 or 2
Penis: eversible → protrusible	?	eversible-protrusible	protrusible	eversible	eversible

ducal gland and its degree of development; and the composition of the penis and its eversibility or protrusibility seem to be the totality of such characters. One would need to know in detail the phylogenetic history of the members of the order, and there are no clear clues to this history offered by the study of the anatomy of the worms or their present distribution, in order to assert that any of these features are primitive (Table 1).

Origins and distributions.—It is probably futile to seek the ancestral stock of the branchiobdellidans among the other clitellates. Stephenson (1930:704–705) regarded them as oligochaetes and derived them from the Lumbriculidae. Holt (1965b) showed that they are not oligochaetes, but said nothing as to their origins. Brinkhurst (in Brinkhurst and Jamieson 1971:169–172, fig. 4.2) argued for the primitive position of the lumbriculids and in his schema of phylogenetic relationships (Brinkhurst and Jamieson 1971:191, fig. 4.4) places the branchiobdellidans next to the former, but otherwise does not mention them. The branchiobdellidans are derived from an ancient stock of the Uroligochaetes, possibly quite different from any living form. The problem cries for restudy with the use of modern techniques, including cyto-chemistry and electron microscopy (see Weigl 1980).

Nonetheless, some speculations as to the origins and historical wanderings of the order and its members deserve, if for no other reason than refutation, brief mention.

The distribution of the families and genera of the branchiobdellidans is not congruent with that of the astacoideans (Holt 1968a:85–86). Holt's speculations therein antedate the general acceptance of the geological theories of plate tectonics and may now be regarded as an example of the efforts of earlier historical zoogeographers to explain the distribution of animals. More credible is Hobbs' (1974:2; 1981:52) belief that the unusual distribution of the families of the Astacoidea is the result of separate invasions of freshwaters by different ancestral marine stocks.

But the branchiobdellidans originated in freshwater: no saline-tolerant branchiobdellidans are known.

The uncertainties of the consequences of

floating and colliding continental land masses (and fragments, "terranes," thereof) and the utter lack of a fossil record preclude any conclusions as to the times of origin prior to the Cretaceous and the subsequent migrations of the branchiobdellidans. They arose in the nothern regions of Pangaea that today are incorporated into the two Holarctic lands.

The branchiobdellidans are an independent group, evolving in response to a myriad of environmental factors, only a few of which are determined by their means of transport. They were most likely adapted to symbiosis with unknown freshwater animals (? crustaceans) when the various stocks of the astacoideans came in out of the sea. They can, thus, hardly be expected to bear the burden of explaining the evolutionary vagaries of their hosts. This is not to deny that plausible theories correlating the distribution of both worms and hosts that now occupy a common area cannot be devised (Hobbs et al. 1967; Holt 1968c, 1969, 1973c, 1974b, inter alia).

Problems of classification.—Any attempt at grouping the genera of the branchiobdellidans into families is not only faced with the usual difficulties of such efforts, but is complicated by an unusual number of apparent convergences. Two such cases are of particular relevance: the penis appears to have evolved from a cuticular eversible tube into a muscular organ that may be either eversible or protrusible in more than one lineage or the opposite; the prostate is of variable development or absent in what otherwise are clearly related groups. These inconsistencies defy all attempts at organization. Two salient features of members of the order are used to derive the arrangement which follows: the number of anterior nephridiopores and the points of entry of the vasa deferentia into the spermiducal gland. The problem of the variations in the structure of the penis and the apparent convergencies presented by these differences may well be solved by more careful studies of the nature of the muscular penes in several genera. (The problem has received little attention and has only recently been broached by Holt (1978a:479; 1982:254).) And the muscular penes of such genera as *Ankyrodrilus* Holt, 1965; *Xironogiton* Ellis, 1919; and *Adenodrilus* Holt, 1977, among others, are different from and may not be homologous with those of the much better known ones of *Cambarincola* Ellis, 1912. If this should prove to be the case, the arrangement presented herein is basically sound (Fig. 2).

One other unrelated difficulty exists: Liu and Zhang (1983) described a Chinese species that they assigned to *Branchiobdella* as *B. heterorchis* with only one pair of testes in segment VI. If there is only one pair of testes in this segment in this species it possibly should be placed in a separate family. Stuart R. Gelder and Liu Si-Cheng (pers. comm.) are considering this in a forthcoming review of east Asian branchiobdellidans. The species will not be further referred to herein. But it is conceivable that work yet to come on the Eurasian fauna will justify the creation of suborders on the basis of the number and location of pairs of testes. For now the characters discussed herein do not clearly require this, though neither do they negate such a classification.

The following, then, is proposed as a suprageneric classification of the branchiobdellidans.

Class Clitellata

Order Branchiobdellida
Family Branchiobdellidae
Bdellodrilidae
Xironodrilidae
Caridinophilidae
Cambarincolidae

Key to the Families and Genera of the Order Branchiobdellida Holt

A key to the then known branchiobdellidan genera of North America was provided by Holt (1978b:292–295) for Pennak's (1978) *Freshwater Invertebrates of the*

United States, but no comprehensive one for all the genera of the order has been published since Goodnight's (1940:28–30) now outdated one. The one presented below is followed by familial and generic synonymies, diagnoses, location of types, ranges, number of species and literature references.

1. Vasa efferentia enter spermiducal gland separately; no vasa deferentia; spermiducal gland globose. Family Caridinophilidae ..... *Caridinophila*
– Vasa efferentia unite to form vasa deferentia; spermiducal gland elongate 2
2. (1) Vasa deferentia enter ental end of spermiducal gland 3
– Vasa deferentia enter ectad to ental end of spermiducal gland 12
3. (2) Some body segments flattened; two anterior nephridiopores. Family Xironodrilidae ..... *Xironodrilus*
– Terete; one anterior nephridiopore. Family Cambarincolidae .. 4
4. (3) Penis eversible cuticular tube ..... *Oedipodrilus*
– Penis ectally a muscular epithelial tube, or connected by strands to inner wall of penial sheath, or densely muscular 5
5. (4) Ectal end of penis cellular epithelial tube enclosing eversible cuticular tube; prostate arises entad to junction of spermiducal gland and ejaculatory duct ..... *Tettodrilus*
– Penis variously muscular 6
6. (5) Penis eversible, connected to inner wall of penial sheath by strands 7
– Penis densely muscular 8
7. (6) Body ornamented with peristomial tentacles and dorsal projections ..... *Ceratodrilus*
– Both without tentacles or dorsal projections ..... *Sathodrilus*
8. (6) Spermiducal gland without a prostate 9
– Prostate or prostatic rudiment associated with spermiducal gland 10
9. (8) Penis composed of muscular, eversible ejaculatory duct ..... *Triannulata*
– Bursa long, muscular; retracted penis short, eversible; spermiducal gland long, slender .. *Magmatodrilus*
10. (8) Spermatheca absent; penis composed of atrial fold.. *Ellisodrilus*
– Spermatheca present; penis protrusible muscular cone 11
11. (10) Prostate incompletely divided from spermiducal gland .. *Pterodrilus*
– Prostate arises at junction of spermiducal gland and ejaculatory duct ..... *Cambarincola*
12. (2) One anterior nephridiopore. Family Bdellodrilidae 13
– Two anterior nephridiopores. Family Branchiobdellidae 15
13. (12) Penis cuticular tube lying free in elongated penial sheath ..... *Cronodrilus*
– Penis muscular 14
14. (13) Penis and penial sheath eversible; ejaculatory duct short, dilated; bursa with pair of glands; spermatheca bifid ..... *Bdellodrilus*
– Penis densely muscular; ejaculatory duct short, with three layers of muscle; no bursal glands; spermatheca without lateral branches ..... *Adenodrilus*
15. (12) Penis cuticular tube; one pair of testes in segment V ..... *Branchiobdella*
– Penis membraneous or muscular 16
16. (15) Penis membraneous, eversible, attached to inner wall of penial sheath by thin strands ... *Cirrodrilus*
– Penis muscular 17
17. (16) Penial sheath eversible; ejaculatory duct short, ectal tip forming protruded penis; ental end of spermiducal gland bifurcated ..... *Ankyrodrilus*
– Bursa asymmetrically spherical enclosing protrusible muscular pe-

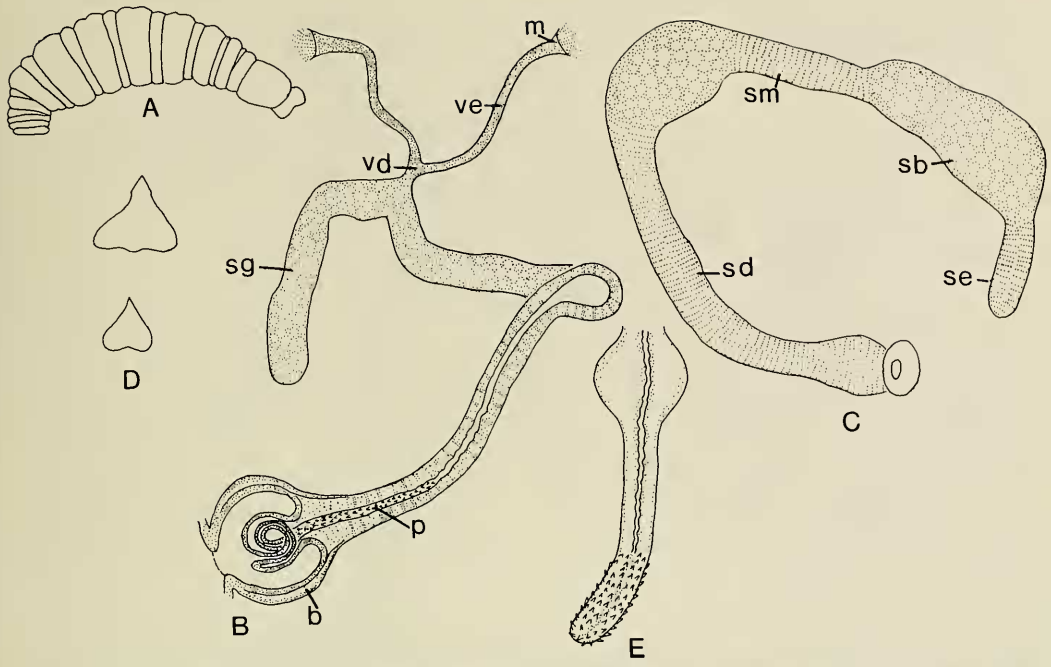

Fig. 3. *Branchiobdella astaci*: A, Lateral view of animal; B, Male efferent apparatus; C, Spermatheca; D, Jaws; E, Tip of everted penis. Abbreviations: b, bursa; m, male funnels; p, penis; sb, spermathecal bulb; sd, ectal duct of spermatheca; se, ental process of spermatheca; sg, spermiducal gland; sm, median duct of spermatheca; ve, vas efferens; vd, vas deferens. (A, B, after Pop 1965:22; C, D, E, after Dorner 1864: plate 37.)

nis; spermatheca vestigial .....
..... *Xironogiton*

Order Branchiobdellida

Clitellate annelids with constant number of segments (15); without setae or prostomium; peristomium forming anterior sucker; with posterior sucker; dorsal and ventral pharyngeal dental placoids; body divided into head of 4 segments, trunk of 11; anus dorsal, subterminal; 2 pairs of nephridia, asymmetrical pair in trunk segments I–IV, symmetrical pair in trunk segments VIII–IX; muscles non-syncytial, composed of cells with outer contractile and inner undifferentiated cytoplasm; testes in trunk segments V and VI or one of these segments only; paired male funnels and ducts in each testicular segment; male efferent apparatus opening through single pore on venter of trunk segment VI; a pair of ovaries and ovipores without oviducts and funnels in trunk segment VII; unpaired spermatheca, if present, in trunk segment V; clitellum on trunk segments VI and VII; Holarctic symbionts of freshwater crustaceans (modified from Holt 1965b:30–31).

Family Branchiobdellidae

Branchiobdellinae Goodnight, 1940:27 (in part).

Diagnosis. —Two anterior nephridiopores; vasa deferentia enter spermiducal gland ectad to latter's ental end; no prostate.

Genus *Branchiobdella*
Fig. 3

Branchiobdella Odier, 1823. [Type species, by subsequent designation (Goodnight 1940:28), *Branchiobdella astaci* Odier 1823:75. Gender; feminine.]

Deposition of type specimens. —Unknown, presumably never designated.

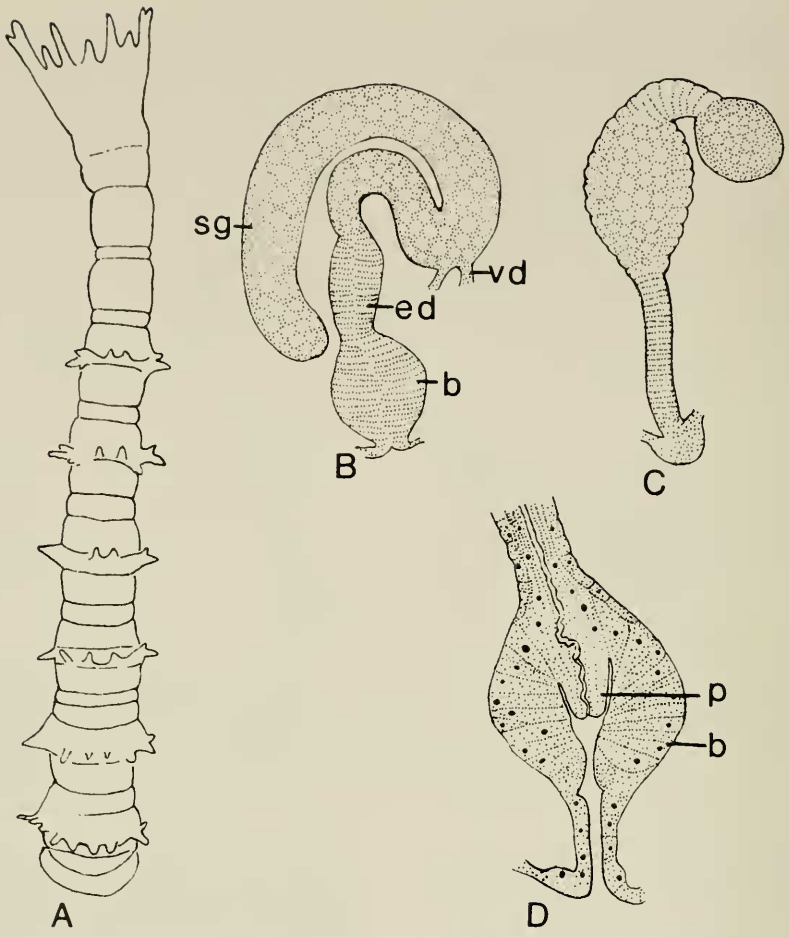

Fig. 4. *Cirrodrilus cirratus*: A, Dorsal view; B, Male efferent apparatus; C, Spermatheca; D, Longitudinal section through bursa and penis. Abbreviations: ed, ejaculatory duct; others as for Fig. 3 (after Yamaguchi 1934, figs. 4, 5).

Diagnosis.—One pair of testes in segment V; penis eversible, cuticular tube.

Range.—Europe; Asia: China, Korea, Japan.

Number of species.—Pop (1965) recognized four species, one with three subspecies; Karaman (1970), six species, two with a subspecies each in Europe; seven east Asian species are accepted as valid by Gelder and Liu (in ms.).

References.—Pierantoni 1906a, 1912; Stephenson 1930; Yamaguchi 1934; Goodnight 1940; Georgevitch 1955, 1957; Pop 1965; Karaman 1970; Gelder and Liu (ms.).

Note.—The literature pertaining to the genus *Branchiobdella* is confusing. The species currently assigned to it in both Europe and Asia may well include more than one genus in both regions.

Genus *Cirrodrilus*
Fig. 4

Cirrodrilus Pierantoni, 1905:2. [Type species, by subsequent designation (Goodnight 1940:63), *Cirrodrilus cirratus* Pierantoni, 1905:1. Gender: masculine.]
Ceratodrilus Yamaguchi, 1932a:361, 366.
Carcinodrilus Yamaguchi, 1932b:62.

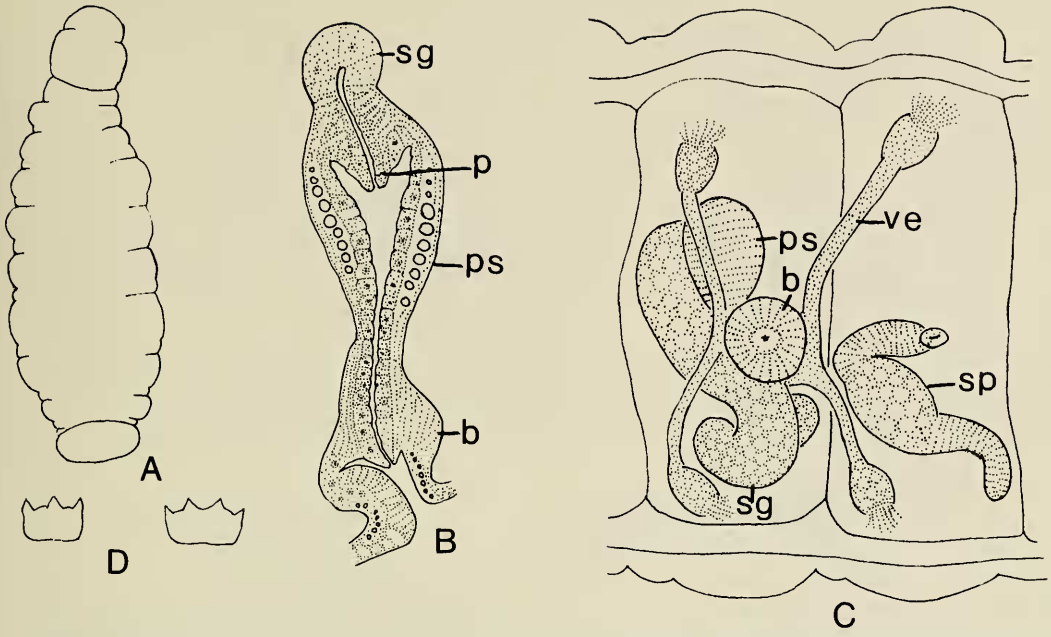

Fig. 5. *Ankyrodrilus koronaeus*: A, Dorsal view; B, Longitudinal section through bursa and penis; C, Ventral view, reproductive systems; D, Jaws, upper to left. Abbreviations: sp, spermatheca; others as above (after Holt 1965a, figs. 6, 9, 1, 4, 5).

Stephanodrilus (*Stephanodrilus*) Yamaguchi, 1934:191–192.

Stephanodrilus (*Ceratodrilus*) Yamaguchi, 1934:191–192.

Cirrodrilus Goodnight, 1940:63; Holt, 1960a:54–57, 1967b:3.

Disposition of type specimens.—Unknown; some of Pierantoni's material is deposited in the Zoologische Museum at Hamburg (Holt 1967b:5).

Diagnosis.—Two pairs of testes in segments V and VI; penis membraneous, eversible, attached by strands to inner wall of penial sheath. [This genus is heterogeneous and should be subdivided. See Yamaguchi 1934:199–200.]

Range.—Asia: Japan, Korea, China.

Number of species.—Twenty-one species are accepted by Gelder and Liu (23, with the removal of *C. truncatus* (Liang, 1963) to a new genus, are proposed in ms. by these authors); other names are available.

References.—Pierantoni 1905, 1906b, 1912; Yamaguchi 1932a, b, 1934; Goodnight 1940; Holt 1960a, 1967b.

Genus *Ankyrodilus*
Fig. 5

Ankyrodrilus Holt, 1965a:10. [Type species, by original designation, *Ankyrodrilus koronaeus* Holt, 1965a:10. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1965a:11).

Diagnosis.—Two pairs of testes; ental end of spermiducal gland bifurcated; penis muscular, penial sheath eversible; ejaculatory duct absent; mid-portion of body depressed.

Range.—Eastern North America: southwest Virginia to middle Tennessee.

Number of species.—Two.

References.—Holt 1965a, Hobbs et al. 1967.

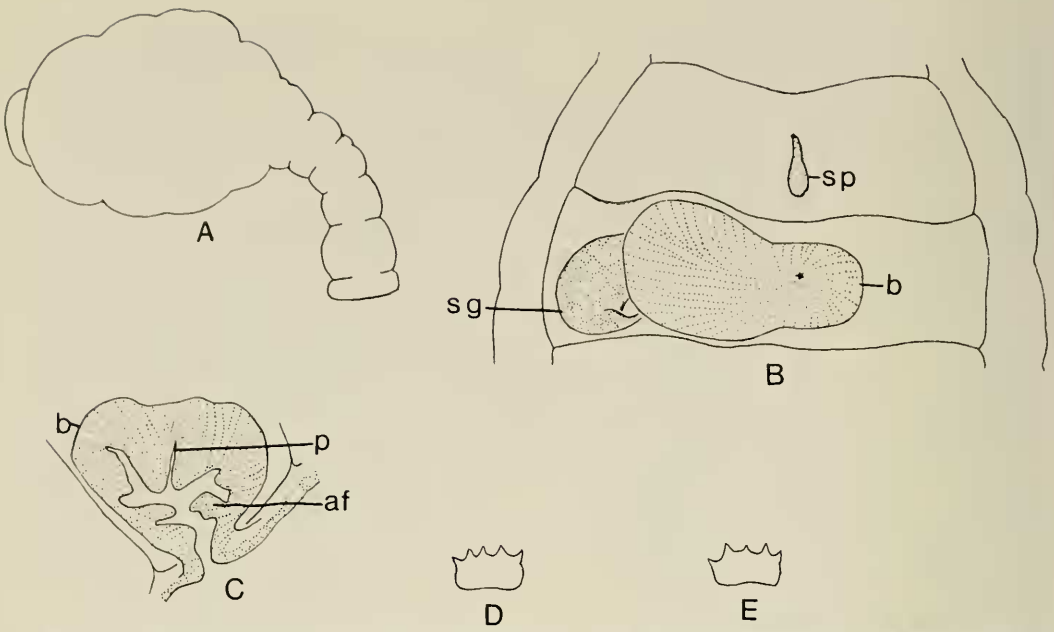

Fig. 6. *Xironogiton instabilis*: A, Dorsal view; B, Ventral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Upper jaw; E, Lower jaw. Abbreviations: af, atrial fold; others as above (after Holt 1974b; fig. 2).

Genus *Xironogiton*
Fig. 6

Xironogiton Ellis, 1919:247. [Type species, by original designation, *Xironogiton oregonensis* Ellis, 1919:248. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Ellis 1919:249).

Diagnosis.—Two pairs of testes; penis, muscular, protrusible; bursa large, spherical to asymmetrical; spermiducal gland not bifurcated entally; spermatheca small; midportion of body depressed.

Range.—North America: higher elevations of Appalachian uplands; north portion of Pacific versant.

Number of species.—Five.

References.—Ellis 1919; Goodnight 1940; Holt 1949, 1974b.

Family Bdellodrilidae

Cambarincolinae Goodnight, 1940:53 (in part).

Diagnosis.—One anterior nephridiopore; vasa deferentia enter spermiducal gland ectad to its ental end; no prostate.

Genus *Bdellodrilus*
Fig. 7

Bdellodrilus Moore, 1895b:498. [Type species, by subsequent designation (Goodnight 1940:53) *Brachiobdella illuminata* Moore, 1894:421. Gender: masculine.]

Disposition of type specimens.—Uncertain; Moore's collections are now in those of the National Museum of Natural History, Smithsonian Institution.

Diagnosis.—Penis eversible, epithelial (Moore 1895b:591, figs. 19, 20); bursa provided with 2 lateral glands enclosed in its muscular wall; spermatheca with lateral process; body wall thin, glandular.

Range.—North America: eastern United States, Mexico.

Number of species.—One.

References.—Moore 1895b, Hobbs et al. 1967; Holt 1973c.

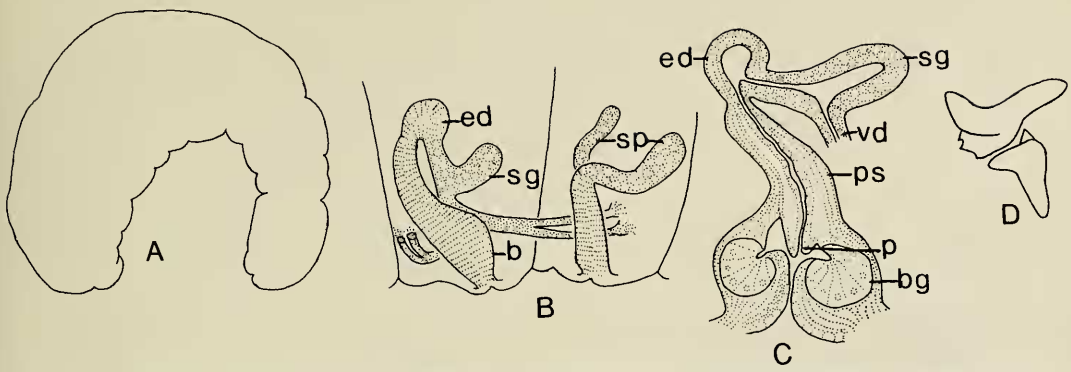

Fig. 7. *Bdellodrilus illuminatus*: A, Lateral view; B, Lateral view, reproductive systems; C, Lateral view of part of male efferent apparatus; D, Jaws. Abbreviations: bg, bursal gland; others as above (B, C, after Moore 1885b, figs. 19, 20; A, D, after Hobbs et al. 1967, fig. 13).

Genus *Cronodrilus*
Fig. 8

Cronodrilus Holt, 1968a:308. [Type species, by original designation, *Cronodrilus ogygius* Holt, 1968a:308. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1968a:308).

Diagnosis.—Penis eversible, cuticular; penial sheath very long; ejaculatory duct short.

Range.—North America: Georgia.

Number of species.—One.

Reference.—Holt 1968a.

Genus *Adenodrilus*
Fig. 9

Adenodrilus Holt, 1977b:727. [Type species, by original designation, *Adenodrilus hemophagus* Holt, 1977b:727.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1977b:727).

Diagnosis.—Penis muscular, (?) eversible; ejaculatory duct composed of 3 layers

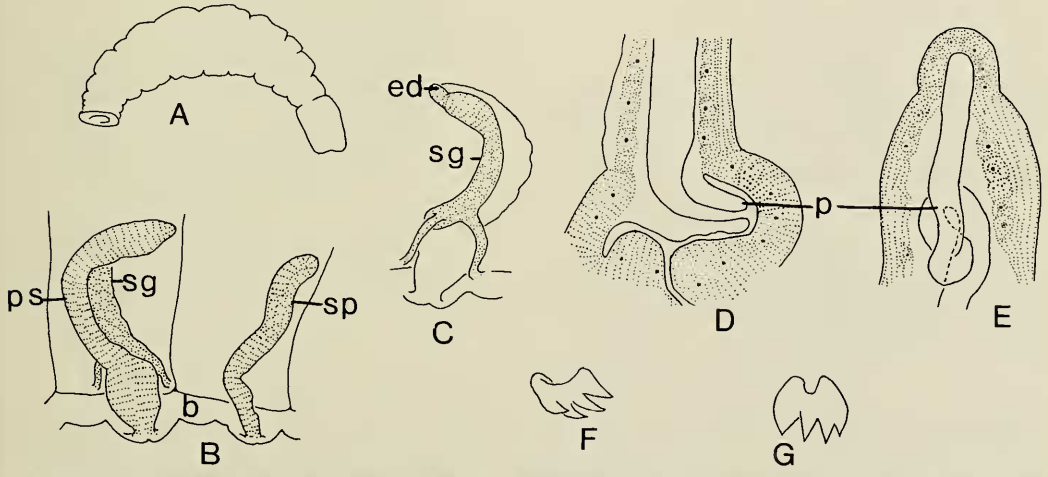

Fig. 8. *Cronodrilus ogygius*: A, Lateral view; B, Lateral view, reproductive systems; C, Lateral view, spermiducal gland; D, Ectal end of penis; E, Ental end of penis; F, Oblique view, upper jaw; G, Oblique view, lower jaw. Abbreviations: as above (after Holt 1968b, figs. 7, 8).

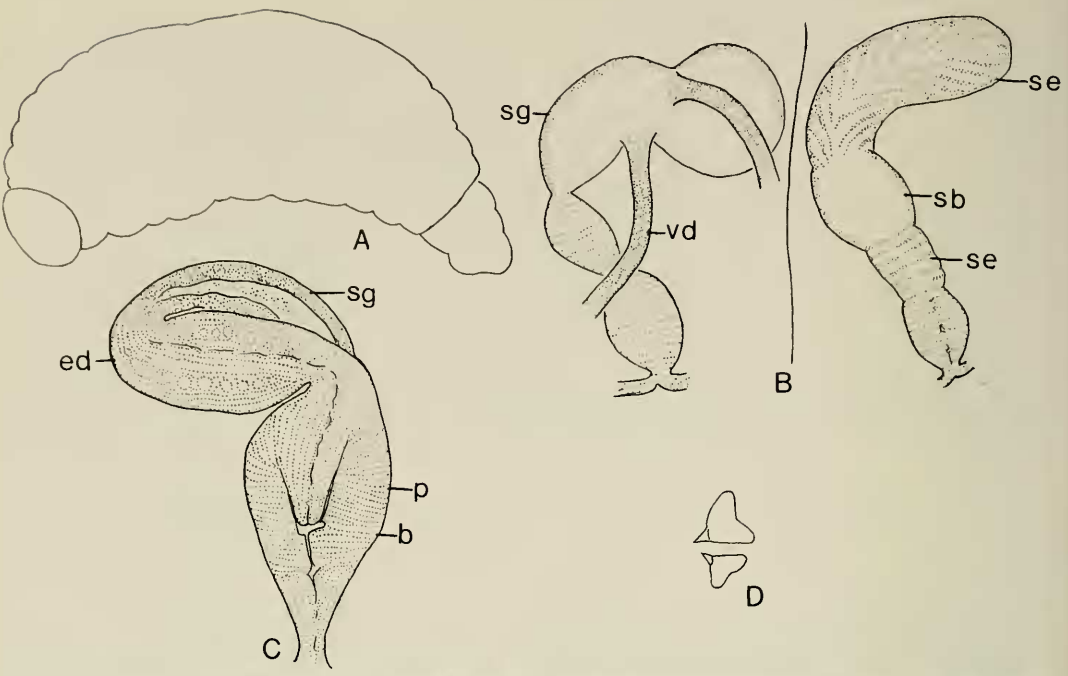

Fig. 9. *Adenodrilus hemophagus*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and ejaculatory duct; D, Jaws. Abbreviations: as above (after Holt 1977b, figs. 1, 3, 5, 2).

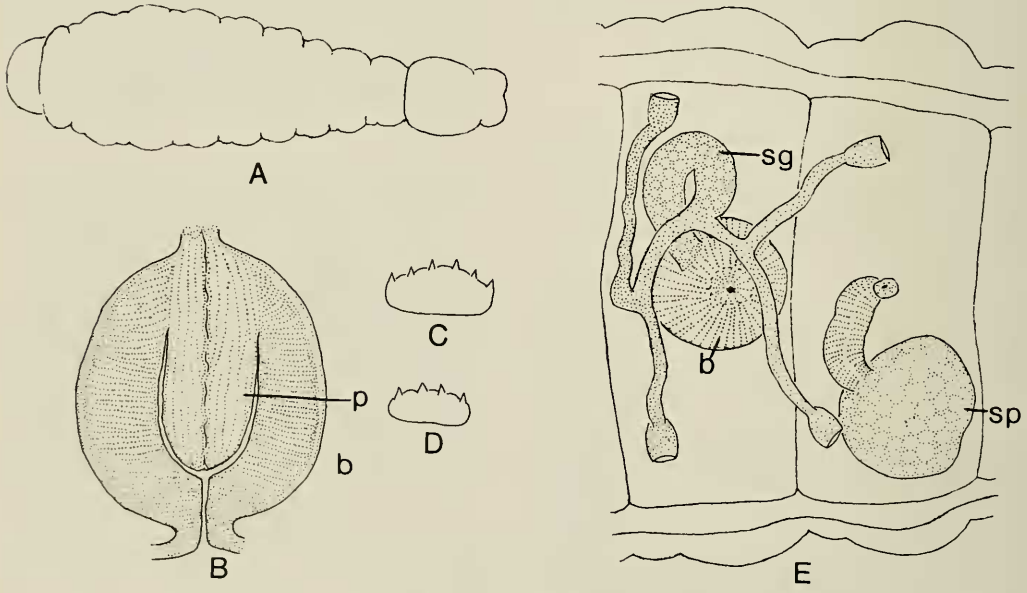

Fig. 10. *Xironodrilus formosus*: A, Dorsal view; B, Longitudinal section through bursa and penis; C, Upper jaw; D, Lower jaw; E, Ventral view, reproductive systems. Abbreviations: as above (original).

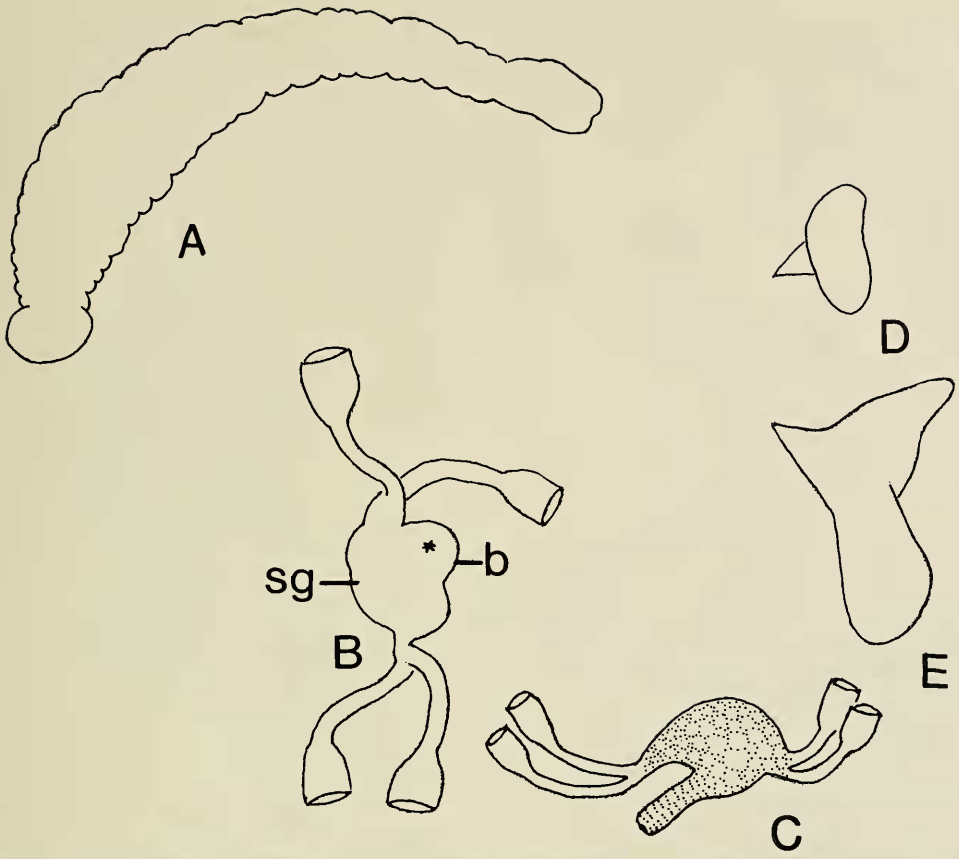

Fig. 11. *Caridinophila unidens*: A, Lateral view; B, Ventrolateral view, male efferent apparatus; C, Same, lateral view, diagrammatic; D, Upper Jaw; E, Lower jaw. Abbreviations: as above (after Liang 1963, fig. 3A, F, I, C, D).

of muscles; spermiducal gland constricted at junction with vasa deferentia; body wall thin, glandular.

Range.—North America: Oregon.

Number of species.—One.

Reference.—Holt 1977b.

Family Xironodrilidae

Cambarincolinae Goodnight, 1940:48 (in part).

Diagnosis.—Two anterior nephridiopores; two pairs of testes; vasa deferentia enter ental end of spermiducal gland; no prostate; penis muscular, protrusible.

Genus *Xironodrilus*

Fig. 10

Xironodrilus Ellis, 1918:49. [Type species, by subsequent designation (Ellis 1919: 244), *Xironodrilus formosus*. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Ellis 1919:244).

Diagnosis.—As for the family; mid-portion of body depressed.

Range.—North America: Michigan southeast to the Piedmont of North Carolina.

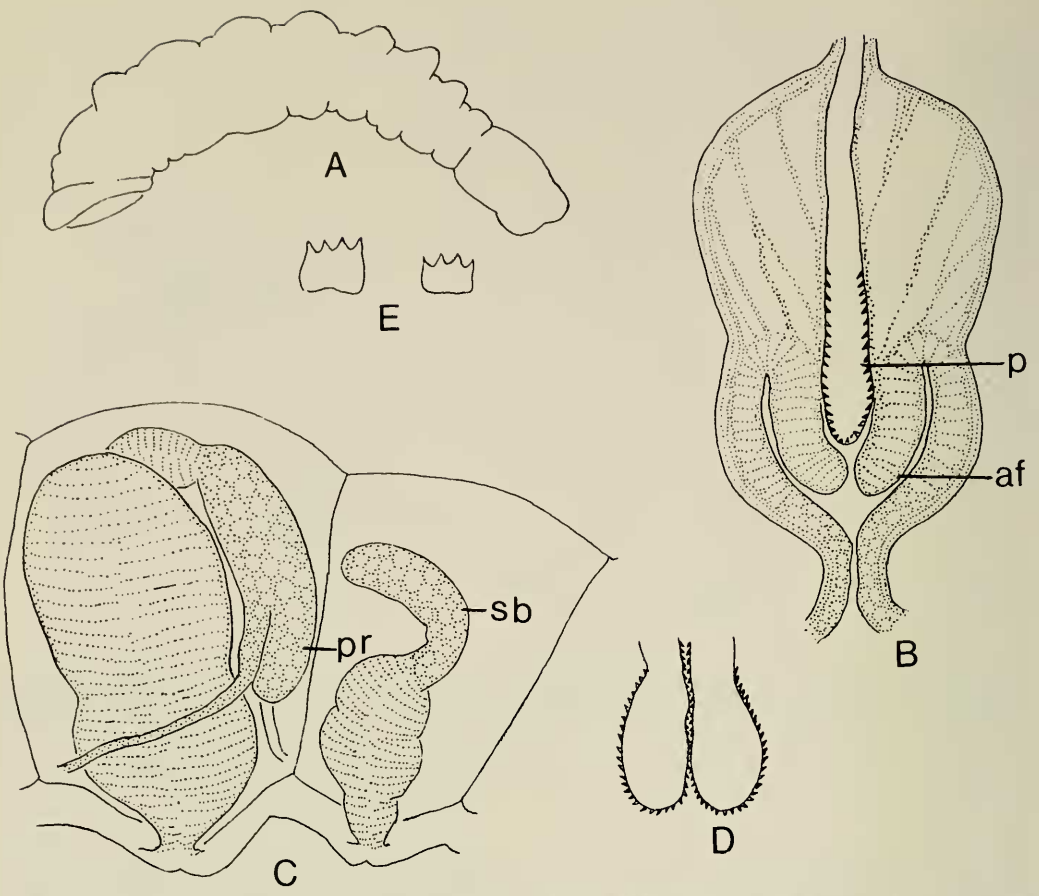

Fig. 12. *Oedipodrilus oedipus*: A, Lateral view; B, Longitudinal section through bursa and penis; C, Lateral view, reproductive systems; D, Tip of partially everted penis; E, Jaws, upper to left. Abbreviations: pr, prostate; others as above (A, C, E, after Holt 1967a; figs. 1, 4, 2, 3; B, D, after Holt 1984a, fig. 3).

Number of species.—Five.

References.—Moore 1894; Ellis 1919; Goodnight 1940, 1943; Holt and Weigl 1979.

Family Caridinophilidae

Diagnosis.—One anterior nephridiopore; 2 pairs of testes; vasa efferentia enter subspherical spermiducal gland separately (no vasa deferentia); no prostate; no spermatheca.

Genus *Caridinophila*
Fig. 11

Caridinophila Liang, 1963:565, 569. [Type species, by original designation, *Caridinophila unidens* Liang, 1963:565. Gender: feminine.]

Disposition of type specimens.—Unknown.

Diagnosis.—As for the family.

Range.—Asia: Yunnan Province, China.

Number of species.—One.

Reference.—Liang 1963.

Family Cambarincolidae

Cambarincolinae, Goodnight, 1940 (in part).

Diagnosis.—One anterior nephridiopore; 2 pairs of testes; vasa deferentia enter ental end of spermiducal gland.

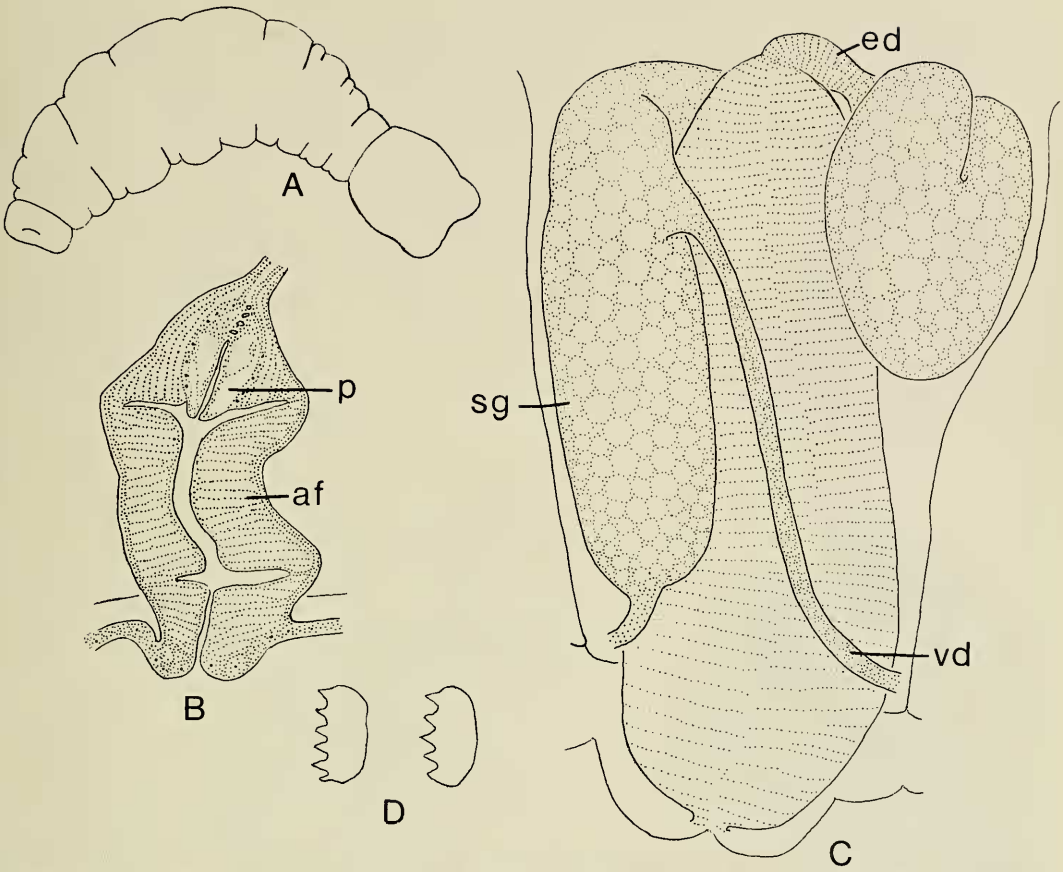

Fig. 13. *Magmatodrilus obscurus*: A, Lateral view; B, Longitudinal section through bursa and penis; C, Lateral view, male efferent apparatus; D, Jaws, upper to left. Abbreviations: as above (A, C, D, after Holt 1967b, figs. 3, 4, 1, 2; B, after Holt 1974a, fig. 4).

Genus *Oedipodrilus*
Fig. 12

Oedipodrilus Holt, 1967a:58. [Type species, by original designation, *Oedipodrilus oedipus* Holt, 1967a:58. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1967a:58).

Diagnosis.—Penis eversible, cuticular, provided with many small recurved hooks; prostate rudimentary to well developed lobe of ental portion of spermiducal gland.

Range.—North America: Kentucky, Tennessee, Mexico.

Number of species.—Three.

References.—Holt 1967a, 1984a.

Genus *Magmatodrilus*
Fig. 13

Magmatodrilus Holt, 1967b:3. [Type species, by original designation (Holt 1967b:3), *Stephanodrilus obscurus* Goodnight, 1940:55. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1967b:3).

Diagnosis.—No prostate, penis short, eversible; bursa large, atrial region elongated; spermiducal gland long.

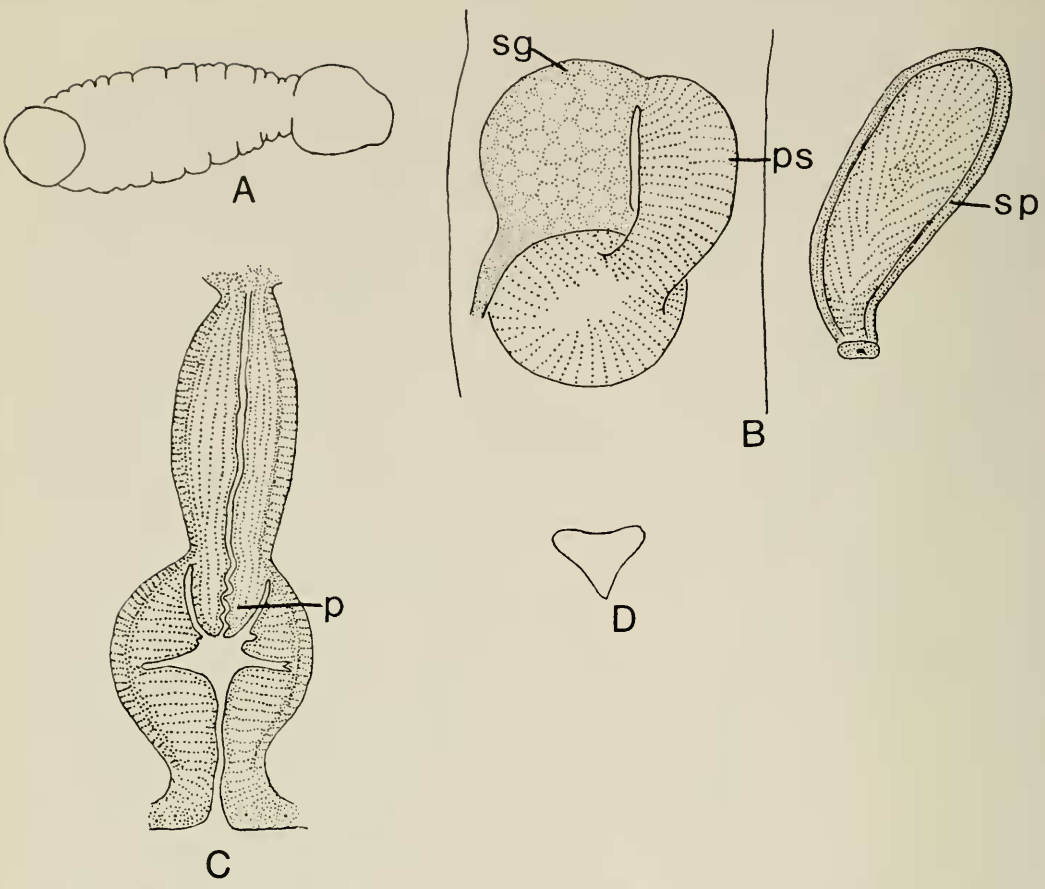

Fig. 14. *Triannulata magna*: A, Lateral view; B, Laterodorsal view, reproductive systems; C, Longitudinal section through bursa and penis; D, Ventral jaw. Abbreviations: as above (after Holt 1974a, figs. 1, 2, 3).

Range.—North America: California.

Number of species.—One.

References.—Goodnight 1940; Holt 1967b, 1974a.

Genus *Triannulata*
Fig. 14

Triannulata Goodnight, 1940:56. [Type species, by original designation, *Triannulata magna* Goodnight, 1940:56. Gender: feminine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Goodnight 1940:57).

Diagnosis.—No prostate; no ejaculatory duct; penis long, muscular, eversible; atrial portion of bursa spherical; spermiducal gland short, subspherical; spermatheca short, muscular.

Range.—North America: Oregon, Washington.

Number of species.—One.

References.—Goodnight 1940, Holt 1974a.

Genus *Ceratodrilus*
Fig. 15

Ceratodrilus Hall, 1914:191. [Type species, by original designation, *Ceratodrilus thysanosomus* Hall, 1914:191. Gender: masculine.]

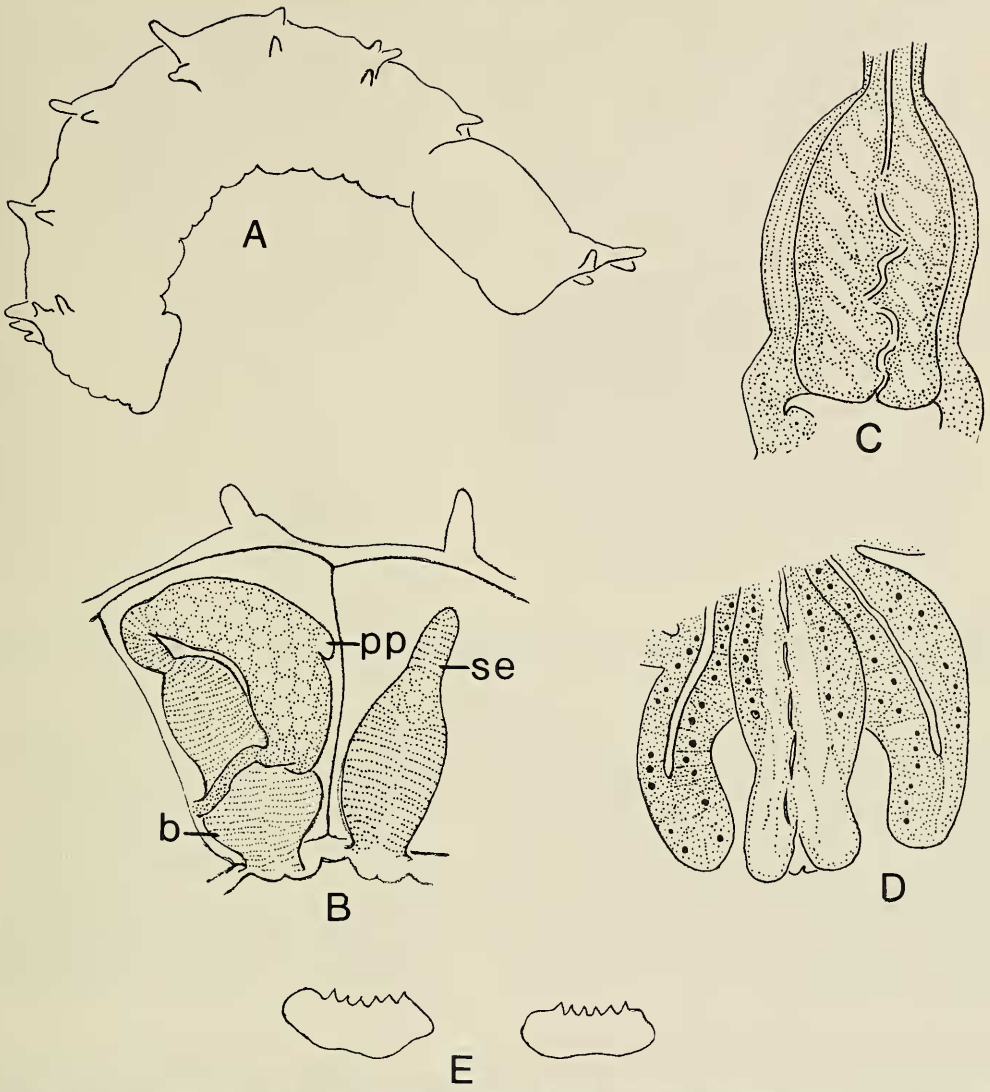

Fig. 15. *Ceratodrilus thysanosomus*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through penial sheath and penis; D, Everted penis; E, Jaws, upper to left. Abbreviations: pp, prostatic protuberance; others as above (after Holt 1960a, figs. 11, 12, 6, 7, 15, 16).

Stephanodrilus (Ceratodrilus) Yamaguchi, 1934:192. [Type species, by subsequent designation (Goodnight 1940:55), *Stephanodrilus sapporensis* Pierantoni, 1906b:3.]

Cirrodrilus Pierantoni, 1905:2. [Type species, by subsequent designation (Goodnight 1940:63), *Cirrodrilus cirratus* Pierantoni, 1905:2.]

Ceratodrilus (Holt, 1960a:53–73).

Disposition of type specimens. — "U.S.N.M. (Bureau of Animal Industry Helminthological Collection" (Hall 1914: 191).

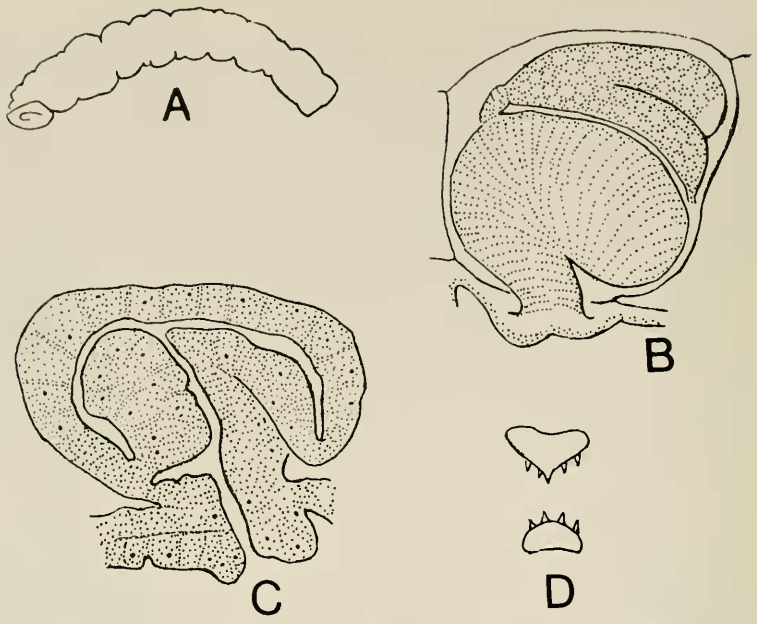

Fig. 16. *Ellisodrilus clitellatus*: A, Lateral view; B, Male efferent apparatus; C, Longitudinal section through bursa; D, Jaws (after Holt 1960b, figs. 1, 2, 3, 4).

Diagnosis.—Digitate projections on dorsum of segments II–VII; peristomium tentaculated; prostatic bulb near ental end of spermiducal gland; penis membraneous, eversible, attached by strands to inner wall of penial sheath; bursa elongate.

Range.—North America: Utah, Idaho, Oregon, Wyoming.

Number of species.—Two.

References.—Hall 1914; Yamaguchi 1934; Goodnight 1940; Holt 1960a.

Genus *Ellisodrilus*
Fig. 16

Ellisodrilus Holt, 1960b:170. [Type species, by original designation, *Ellisodrilus clitellatus* Holt, 1960a:170. Gender: masculine.]

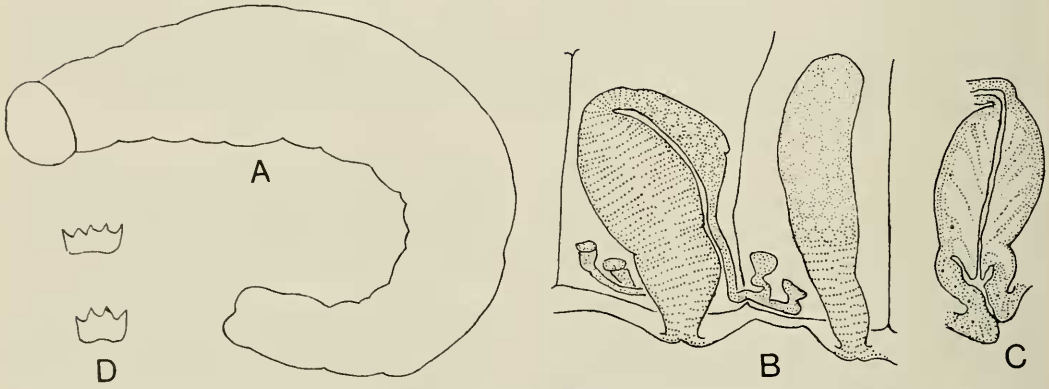

Fig. 17. *Sathodrilus carolinensis*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Jaws (after Holt 1968b, figs. 2, 1).

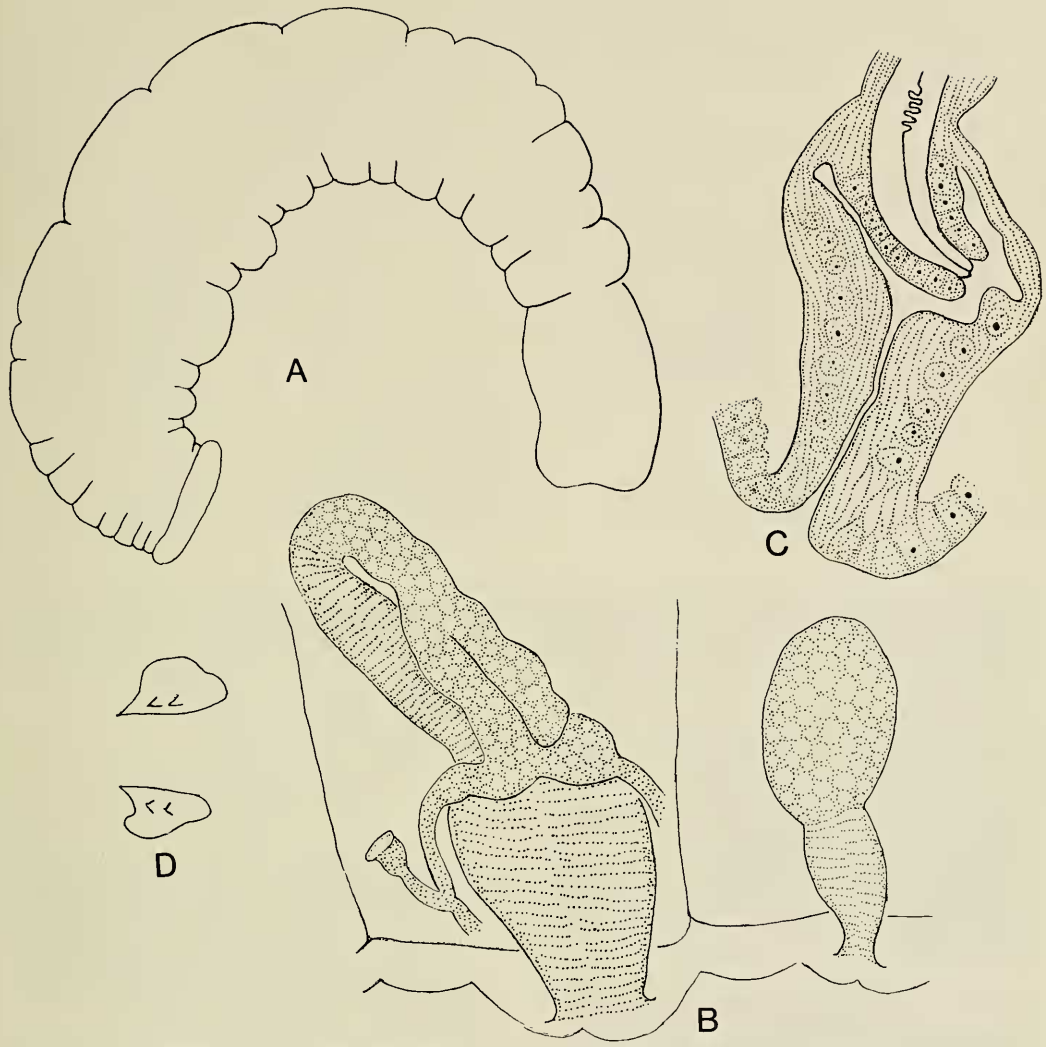

Fig. 18. *Tettodrilus friaufi*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Jaws (after Holt 1968b, fig. 9).

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1960b:170).

Diagnosis.—Prostate arises from mid-portion of spermiducal gland; penis reduced to pore on ectal surface of penial sheath; bursa asymmetrically subspherical; no spermatheca.

Range.—North America: Kentucky, Indiana, Michigan.

Number of species.—Two.

Reference.—Holt 1960b.

Genus *Sathodrilus*
Fig. 17

Sathodrilus Holt, 1968b:294. [Type species, by original designation, *Sathodrilus carolinensis* Holt, 1968b:294. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1968b:294).

Diagnosis.—Prostatic protuberance, or prostate arising along mid-portion of sper-

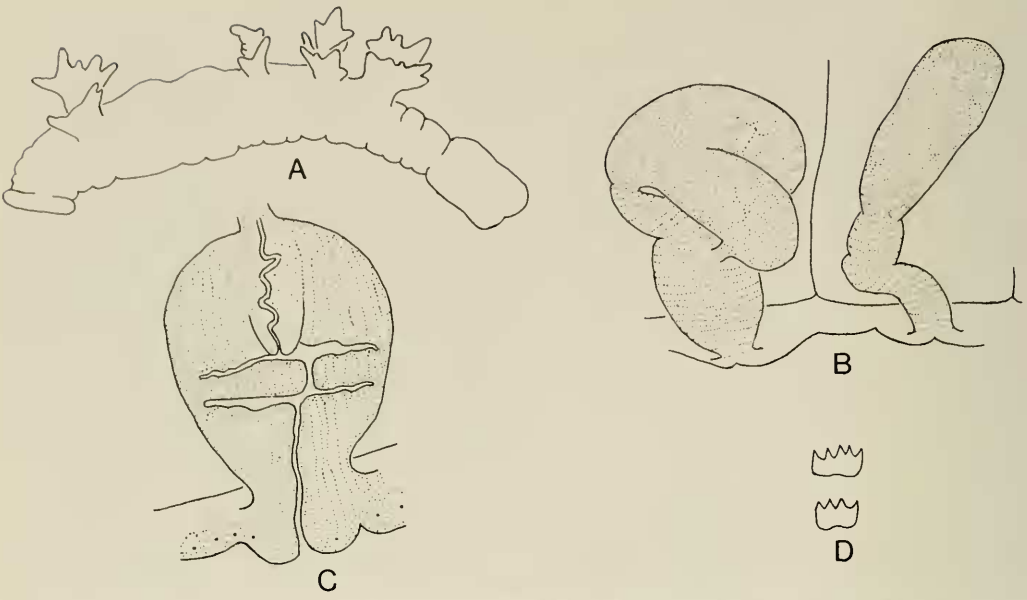

Fig. 19. *Pterodrilus alcicornus*: A, Lateral view; B, Lateral view, reproductive systems; C, Longitudinal section through bursa and penis; D, Jaws (A, B, from Holt 1968c, fig. 7; C, D, original).

miducal gland or absent; penis membraneous, attached by strands to inner wall of penial sheath; bursa usually elongate; dorsal body surface without digitate projections.

Range.—North America.

Number of species.—Fifteen.

References.—Holt 1968b, 1973b, 1977a, 1978a, 1981b.

Genus *Tettodrilus*
Fig. 18

Tettodrilus Holt, 1968b:312. [Type species, by original designation, *Tettodrilus friaufi* Holt, 1968b:314. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Holt 1968b:312).

Diagnosis.—Penis eversible, cuticular; ejaculatory duct projects as epithelio-muscular tube into atrium of bursa, enclosing ectal (when retracted) portion of penis; prostate arises at mid-portion of slender spermiducal gland.

Range.—North America: Tennessee.

Number of species.—One.

Reference.—Holt 1968b.

Genus *Pterodrilus*
Fig. 19

Pterodrilus Moore, 1895a:449. [Type species, by subsequent designation (Goodnight 1940:58), *Pterodrilus alcicornus* Moore, 1895a:449. Gender: masculine.]

Disposition of type specimens.—(?) Lost (Holt 1968c:6).

Diagnosis.—Anterior annulus of segment VIII with elevated dorsal ridge, those of other segments often so, some or all such ridges often with fan-like digitate projections; small worms; prostate arising at mid-portion of short spermiducal gland; penis muscular, protrusible; bursa ovoid to pyriform.

Range.—North America: eastern United States.

Number of species.—Eight.

References.—Moore 1895a; Ellis 1919; Goodnight 1940; Holt 1968c, 1973c.

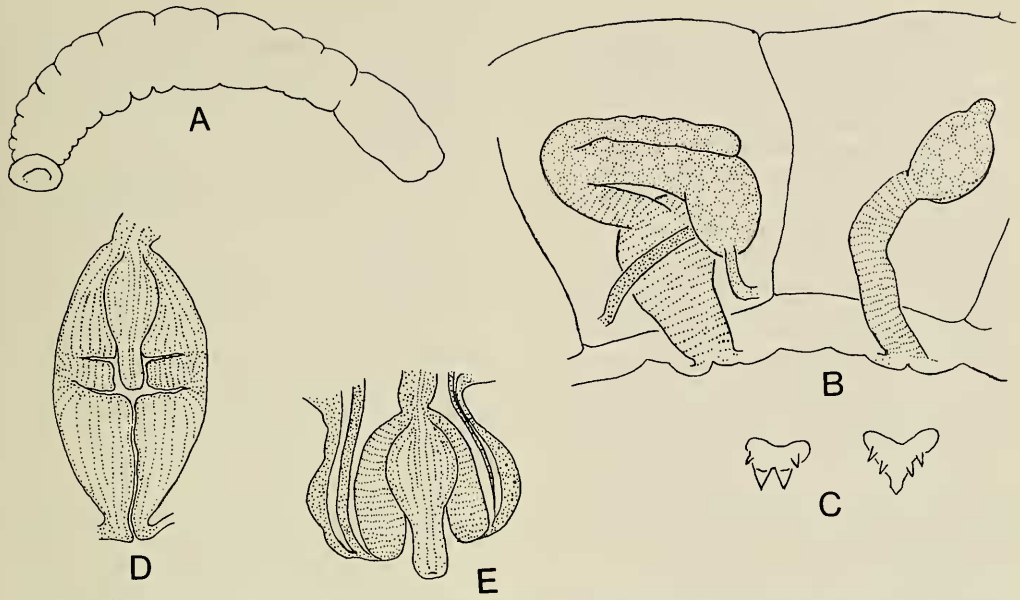

Fig. 20. *Cambarincola macrodontus*: A, Lateral view; B, Lateral view, reproductive systems; C, Jaws (after Holt and Hoffman 1959, figs. 1, 2, 4, 3). *Cambarincola illinoisensis*: D, Longitudinal section through bursa and penis; E, Everted bursa, protruded penis (after Holt 1982, fig. 1D, E).

Genus *Cambarincola*
Fig. 20

Cambarincola Ellis, 1912:481. [Type species, by original designation, *Cambarincola macrodontus* Ellis, 1912:481. Gender: masculine.]

Disposition of type specimens.—National Museum of Natural History, Smithsonian Institution (Ellis 1912:451).

Diagnosis.—Prostate arising at ectal end (junction with ejaculatory duct) of spermiducal gland; penis muscular, protrusible; body segments often with raised anterior annuli (dorsal ridges), never with fan-like or digitate projections.

Range.—North America; introduced into Japan.

Number of species.—Forty-seven.

References.—Ellis 1912, 1919; Goodnight 1940; Hoffman 1963; Holt 1949, 1954, 1963, 1964, 1973b, c, d, e, 1974a, 1978a, 1981a, 1982, 1984a, b; Leidy 1851.

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